When to stay and when to leave? Proximate causes of dispersal in an endangered social carnivore

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Abstract: Reliable estimates of birth, death, emigration and immigration rates are fundamental to understanding and predicting the dynamics of wild populations and, consequently, inform appropriate management actions. However, when individuals disappear from a focal population, inference on their fate is often challenging. Here we used 30 years of individual-based mark–recapture data from a population of free-ranging African wild dogs Lycaon pictus in Botswana and a suite of individual, social and environmental predictors to investigate factors affecting the decision to emigrate from the pack. We subsequently used this information to assign an emigration probability to those individuals that were no longer sighted within their pack (i.e. missing individuals). Natal dispersal (i.e. emigration from the natal pack) showed seasonal patterns with female dispersal peaking prior to the mating season and male dispersal peaking at the beginning of the wet season. For both sexes, natal dispersal rate increased in the absence of unrelated individuals of the opposite sex in the pack. Male natal dispersal decreased with increasing number of pups in the pack and increased in larger packs. Female natal dispersal decreased with increasing number of pups in larger packs, but increased with increasing number of pups in smaller packs. Individuals of both sexes were less likely to exhibit secondary dispersal (i.e. emigration from a pack other than the natal pack) if they were dominant and if many pups were present in the pack. Our models predicted that 18% and 25% of missing females and males, respectively, had likely dispersed from the natal pack, rather than having died. A misclassification of this order of magnitude between dispersal and mortality can have far-reaching consequences in the evaluation and prediction of population dynamics and persistence, and potentially mislead conservation actions. Our study showed that the decision to disperse is context-dependent and that the effect of individual, social and environmental predictors differs between males and females and between natal and secondary dispersal related to different direct and indirect fitness consequences. Furthermore, we demonstrated how a thorough understanding of the proximate causes of dispersal can be used to assign a dispersal probability to missing individuals. Knowledge of causes of dispersal can then be used within an integrated framework to more reliably estimate mortality rates.

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When to stay and when to leave? Proximate causes of dispersal in an endangered social carnivore

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ABSTRACT

1. Reliable estimates of birth, death, emigration, and immigration rates are fundamental to understanding and predicting the dynamics of wild populations and, consequently, inform appropriate management actions. However, when individuals disappear from a focal population, inference on their fate is often challenging.
2. Here we used 30 years of individual-based mark-recapture data from a population of free-ranging African wild dogs (*Lycaon pictus*) in Botswana and a suite of individual, social, and environmental predictors to investigate factors affecting the decision to emigrate from the pack. We subsequently used this information to assign an emigration probability to those individuals that were no longer sighted within their pack (i.e. missing individuals).
3. Natal dispersal (i.e. emigration from the natal pack) showed seasonal patterns with female dispersal peaking prior to the mating season and male dispersal peaking at the beginning of the wet season. For both sexes, natal dispersal rate increased in the absence of unrelated individuals of the opposite sex in the pack. Male natal dispersal decreased with increasing number of pups in the pack and increased in larger packs. Female natal dispersal decreased with increasing number of pups in larger packs, but increased with increasing number of pups in smaller packs. Individuals of both sexes were less likely to exhibit secondary dispersal (i.e. emigration from a pack other than the natal pack) if they were dominant and if many pups were present in the pack.
4. Our models predicted that 18% and 25% of missing females and males, respectively, had likely dispersed from the natal pack, rather than having died. A misclassification of this order of magnitude between dispersal and mortality can have far-reaching consequences in the evaluation and prediction of population dynamics and persistence, and potentially mislead conservation actions.
5. Our study showed that the decision to disperse is context-dependent and that the effect of individual, social, and environmental predictors differs between males and females

and between natal and secondary dispersal related to different direct and indirect fitness consequences. Furthermore, we demonstrated how a thorough understanding of the proximate causes of dispersal can be used to assign a dispersal probability to missing individuals. Knowledge of causes of dispersal can then be used within an integrated framework to more reliably estimate mortality rates.

INTRODUCTION

Understanding and predicting the dynamics of wild animal populations, the foundation upon which many conservation management actions are based, depends on the ability to accurately estimate key demographic rates such as birth, death, emigration, and immigration (Griffith, Salguero-Gómez, Merow, & McMahon, 2016). Reliable empirical information on rates of death and emigration is, however, often difficult to obtain because individuals that disappear from the study population (hereafter referred to as missing individuals) may have either dispersed or died. This is particularly relevant for species that move and disperse over large areas and for which death is rarely observed. In such instances, missing individuals are often assumed dead (i.e. apparent mortality), resulting in underestimation of both true survival and emigration and consequently biasing the representation of overall population dynamics (Furrer & Pasinelli, 2016; Marshall, Diefenbach, Wood, & Cooper, 2004).

A thorough understanding of the proximate causes of dispersal can be instrumental in disentangling emigration from death, for knowing what influences the decision to emigrate offers the possibility to assign a dispersal probability to missing individuals. This knowledge can in turn be used to more reliably estimate mortality rates within a hierarchical framework (Barthold, Packer, Loveridge, Macdonald, & Colchero, 2016) in which the fate of missing individuals is treated as a latent state that gets inferred based on the joint likelihood of emigration and death. Both likelihoods can be calculated on the basis of empirical

74 information, even when partly incomplete. Therefore, understanding under what
75 circumstances individuals decide to emigrate constitutes the first step towards a reliable
76 mortality estimation.
77
78 Several individual, social, and environmental factors have been shown to influence the
79 decision to emigrate. At the individual level, emigration can be influenced by physiological
80 traits, body condition, and age (Clobert, Baguette, Benton, & Bullock, 2012; Maag et al.,
81 2019). Despite dispersal being typical of younger individuals, it may occur at any age, for
82 example following breeding failure (Rioux, Amirault-Langlais, & Shaffer, 2011). The timing of
83 emigration may reflect a trade-off between increasing dispersal ability (e.g. body size) and
84 decreasing prospects for successful reproduction and may thus be mediated by seasonal
85 constraints such as the mating season (Clobert et al., 2012; Shaw & Kokko, 2014). At the
86 social level, emigration is generally explained as a strategy to avoid inbreeding (Clobert et
87 al., 2012; Greenwood, 1980), reduce competition for food and mates (Bonte et al., 2012;
88 Greenwood, 1980), and can vary substantially between sexes and at different population
89 densities (Maag, Cozzi, Clutton-Brock, & Ozgul, 2018). When potential mating partners are
90 limited to close relatives, dispersal can arise because of the fitness consequences that result
91 in inbreeding avoidance behaviours (Lehmann & Perrin, 2003; Wolff, 1992). Furthermore,
92 emigration can be influenced by adult sex ratio, for the scarcity of one sex increases mate
93 competition for the more common sex (Greenwood, 1980). Depending on circumstances,
94 high population density can motivate individuals to either emigrate and avoid increased
95 resource competition in the natal area (Fattebert, Balme, Dickerson, Slotow, & Hunter, 2015;
96 Kim, Torres, & Drummond, 2009), or remain philopatric due to Allee effects or conspecific
97 attraction (Roland, Keyghobadi, & Fownes, 2000; Woodroffe, O'Neill, & Rabaiotti, 2019).
98 Finally, at the level of the environment, the decision to emigrate can be influenced by habitat
99 quality (Bates, Sadler, & Fowles, 2006) and availability of resources such as food (Bonte,
100 Lukáč, & Lens, 2008; Fattebert, Perrig, Naef-Daenzer, & Grüebler, 2019) or space (Bowler &
101 Benton, 2005).

The endangered African wild dog (*Lycaon pictus*) lives in packs from which individuals often disappear and, due to the logistic constraints of monitoring them, information on whether they have emigrated or died is difficult to obtain (Woodroffe & Sillero-Zubiri, 2012). Wild dogs form cooperative breeding packs of up to 40 individuals composed of a dominant pair that monopolises the majority of reproduction, several typically related subordinate adults that help in raising the pups, and a litter of newborn pups (Malcolm & Marten, 1982). Conservation management for the species is of high priority and relies on our ability to correctly quantify population trends and project long-term population dynamics and viability. However, since wild dogs range over large areas (Gittleman & Harvey, 1982), can disperse far beyond most focal study areas (Cozzi et al., 2020; Davies-Mostert et al., 2012; Masenga et al., 2016), and cases of death are rarely observed, information on rates of emigration and mortality are imprecise. Although previous studies have focused on various aspects of dispersal in wild dogs, little is known about the proximate causes of emigration.

Therefore, our aims were to (1) derive an empirical model reflecting proximate causes of emigration in the African wild dog based on known dispersal events and (2) use this information to assign a dispersal probability to missing individuals. To this end, we used 30 years of individual-based capture-recapture data and over 180 dispersal events from a free-ranging population of wild dogs in northern Botswana. We expected a positive relationship between dispersal rate and the degree of relatedness to individuals of the opposite sex within a pack, for wild dogs generally avoid mating with familiar close kin (Girman, Mills, Geffen, & Wayne, 1997). We anticipated the above effect to vary depending on how many same-sex adults are present in a pack as the number of “potential competitors” for the breeding position changes. We predicted dispersal to increase with increasing number of pups, for pups are given priority of access at kills (Malcolm & Marten, 1982) thus increasing within group food competition. On the other hand, we expected a negative relationship between dispersal rate and group size as hunting success (Creel & Creel, 1995; Hubel et al.,

2016) and per capita food intake (Creel & Creel, 2002) increase with group size. We expected the above effects to be more pronounced during the dry season, when food availability is scarce (Pole, Gordon, Gorman, & MacAskill, 2004), and thus also anticipated dispersal to vary seasonally. Furthermore, we predicted a positive relationship between the rate of natal dispersal and the number of same-sex siblings due to group hunting benefits (Creel & Creel, 1995; Hubel et al., 2016) and increased predator vigilance (McNutt, 1996a) gained from dispersing in larger coalitions.

MATERIALS AND METHODS

Study area

The study area is located in the southeastern Okavango Delta of northern Botswana and spans roughly 2,700 km^2 confined by the Khwai River in the north, the Maun-Sankuyo-Mababe regional road in the east, the Southern Buffalo fence in the south, and the Santantadibe River in the west. The habitat is a mosaic of swamps, rivers, riverine forests, woods, savannas, and grasslands. Rainfall is seasonal (November to March) and out of phase with the annual flood that comes from the catchment area of the Cubango and Kavango Rivers in Angola and reaches the study area around June (Mendelsohn et al., 2010). Further details about the study area can be found elsewhere (Cozzi, Broekhuis, McNutt, & Schmid, 2013; McNutt, 1996b).

Data collection

Data were collected between 1989 and 2019 on a free-ranging population of African wild dogs (McNutt, 1996b; McNutt & Silk, 2008). During any given year, between six and twelve wild dog packs were regularly monitored. Packs were visited at least once every five months, but often several times a month (in 92% of all sightings; Appendix S1). At each visit, information on date, coordinates, group composition, health status, reproductive status, and

158 other behaviours were recorded. Individuals were identified based on unique pelage colour
159 markings (Maddock & Mills, 1994). Age and degree of relatedness were known for all
160 individuals born in the monitored packs. Maternity was obvious and assigned to the pregnant
161 and nursing female, which in the majority of the cases (i.e. 86% of litters) was the dominant
162 female. Although extra-pair paternity has been reported (Creel, Creel, Mills, & Monfort, 1997;
163 Spiering, Somers, Maldonado, Wildt, & Gunther, 2010) paternity was by default assigned to
164 the dominant male. Following Jackson, Groom, Jordan, & McNutt (2017), two individuals
165 were defined as being related if the relatedness coefficient was ≥ 0.25, and unrelated
166 otherwise. Individuals that were not born within the monitored packs and that immigrated into
167 the study population were considered as unrelated to all other dogs.
168
169 **Definition of dispersal**
170 New wild dog packs form when same-sex dispersing coalitions (i.e. small groups of sisters or
171 brothers), or single individuals, emigrate from their pack and join unrelated dispersing
172 coalitions of the opposite sex (Fuller, Mills, Borner, Laurenson, & Kat, 1992; McNutt, 1996b;
173 Woodroffe, Rabaiotti, & O'Neill, 2019). Wild dogs mainly disperse from their natal pack at
174 one or two years of age to form a new group in which they can obtain direct fitness (McNutt,
175 1996b; Woodroffe, Rabaiotti, et al., 2019). Some individuals also undertake secondary
176 dispersal from their newly formed packs, likely following failure in acquiring dominance
177 (Creel & Creel, 2002; Fuller et al., 1992; Girman et al., 1997; McNutt, 1996b; Woodroffe,
178 Rabaiotti, et al., 2019). Occasionally, all members of one sex disperse resulting in a
179 permanent breakup of the pack (Woodroffe, Rabaiotti, et al. 2019; Creel & Creel, 2002).
180 Depending on these dispersal types, we expected the potential individual, social, and
181 environmental predictors to affect the dispersal decision differently. We thus distinguished
182 between *natal dispersal* (i.e. emigration from the natal pack), *secondary dispersal* (i.e.
183 emigration from a pack other than the natal pack), and *pack breakup* (i.e. all members of one
184 sex left the pack) in analyses described below.
185

We defined an individual as having dispersed if it was seen away from its pack either on its own, in a same-sex coalition, or in a different pack. After having dispersed, individuals/coalitions equipped with a radio-collar were located using information sent by the collars, while uncollared individuals were identified based on unique pelage colour markings in direct observations or from photographs from tourists and other people active in the area.

We considered data from a total of 180 packs (corresponding to 223 pack years) and 859 known adult wild dogs in our analyses. Overall, we observed natal dispersal for 242 known-aged individuals (132 females, 110 males) in 108 dispersing coalitions from 31 packs; secondary dispersal for 42 wild dogs (23 females, 19 males) in 31 dispersing coalitions from 22 packs; and 52 pack breakup events (Table S1).

Predictors

At each sighting, we recorded for every adult wild dog in the pack (hereafter referred to as candidate disperser) information on dominance status, whether or not all pack members of the opposite-sex were related, number of adults (i.e. pack size), number of pups, age of pups, and number of same-sex adults and siblings. We calculated wild dog population density (individuals/km2) by dividing the total number of known resident adults (aged ≥ 12 months) by the size of the study area. In northern Botswana, reproduction is seasonal and pups are usually born in June (McNutt, Groom, & Woodroffe, 2019). Therefore, we estimated annual population densities right before the onset of reproduction (i.e. early June), when all dogs were approximately ≥ 12 months old. We calculated the sex ratio of all adult wild dogs in the study population (updated each June) as the ratio of resident males to resident females. For each sighting, we estimated the time (constrained between 0-12 months) since June, which corresponds to peak whelping time (McNutt et al., 2019), to account for seasonal effects in the timing of dispersal. To assess the influence of environmental predictors on dispersal rate, we calculated rainfall for each sighting as cumulative precipitation over the prior three months. For this purpose, we used monthly precipitation

data for the spatial extent of the study area provided by Funk et al. (2015), which incorporates 0.05° (i.e. approximately 10x10 km) resolution satellite imagery with in-situ weather station data to create gridded rainfall time series. All parameter calculations and statistical analyses were performed in R, version 3.6.1 (R Core Team, 2019).

Statistical analyses

We investigated the influence of individual, social, and environmental predictors on probability of (1) natal dispersal, (2) secondary dispersal, and (3) pack breakup by fitting separate proportional hazard (PH) models with 'hazard' – the event of interest – referring to dispersal or pack breakup, respectively. We interval-censored our data, as the time interval between consecutive pack sightings varied and the exact timing of an event (i.e. potential dispersal or pack breakup) was unknown (Appendix S1). We applied fully parametric PH (FPPH) models, instead of semi-parametric Cox PH models, because FPPH models directly accommodate interval-censored data (Kleinbaum & Klein, 2010). The proportional hazard model, which represents the instantaneous propensity of an individual to disperse (or of a pack to break up) per unit time, is the product of the baseline hazard function, which may be modelled using different time scales (Fieberg & Delgiudice, 2009), and a set of predictors (Kleinbaum & Klein, 2010) (Appendix S2). We fitted FPPH models with six different parametric baseline hazard functions (i.e. exponential, Weibull, inverse Weibull, Gompertz, lognormal, or log-logistic distribution) implemented in the *R* package *parfm* (Munda, Rotolo, & Legrand, 2012). To account for within-pack correlations, we further included a shared frailty component as a multiplicative random effect, parameterised with either gamma, inverse Gaussian, positive stable, lognormal, or log-logistic distributions (Munda et al., 2012). We used time-dependent predictors that were updated at the beginning of each time interval of sighting. In all cases, we assumed that censoring was random and independent of the event. To test for violations of the PH assumption for each predictor, we extended our models to contain interaction of the focal predictor and time, and we evaluated whether the interaction had a statistically significant effect (Kleinbaum & Klein, 2010). Lastly, in order to

quantify correlates of (4) dispersing group size, we fitted a generalized linear-mixed model (GLMM) with Poisson response using the *R* package *lme4* (Bates, Mächler, Bolker, & Walker, 2014). In all our analyses, we only considered two-way interactions.

For all models (1-4), we standardised continuous predictors and checked for collinearities using Pearson correlation (Dormann et al., 2013). We followed a backward selection procedure based on Akaike Information Criterion (AIC) to find the most parsimonious model (Burnham & Anderson, 2002). Finally, we evaluated the predictive performance of each model on the basis of the area under the receiver operating characteristic curve (AUC) following block cross-validation (Roberts et al., 2016) (Appendix S3). A model that does not perform better than chance has an AUC of 0.5. An AUC value ≥ 0.6 is considered as poor, ≥ 0.7 as good, ≥ 0.8 as excellent, and ≥ 0.9 as outstanding (Hosmer & Lemeshow, 2000).

Natal dispersal (model 1)

We investigated the rate of natal dispersal at the individual level by considering all wild dogs ≥ 12 months old and for which birthdate and natal pack identity were known (i.e. 334 males, 310 females). Individuals that died or had not yet dispersed at the end of data collection were right-censored (Kleinbaum & Klein, 2010). Likewise, we right-censored individuals that dispersed following pack breakup as well as individuals that had gone missing from the natal pack with unknown fate (Table S1). Missing individuals may actually have dispersed and, in such instances, censoring is informative and non-random (Kleinbaum & Klein, 2010). To avoid censoring bias, we thus right-censored missing individuals one time step prior to disappearance. We applied a separate FPPH model for both sexes with an age-based (months since birth) time scale and natal group identity as a shared frailty component to account for unobserved factors at the pack level. To assess the effect of predictors on dispersal rate, we included number of pups, number of adults (i.e. pack size), number of younger adults, number of same-sex siblings, whether or not all pack members of the opposite sex were related, population density, population sex ratio, rainfall, and time since

last reproduction as well as biologically meaningful interactions in our full model (Appendix S4).

Secondary dispersal (model 2)

To investigate the rate of secondary dispersal, we considered all adult wild dogs (i.e. 221 males, 186 females) in a pack other than their natal pack. These individuals were either pack founders (following natal dispersal) or immigrants into an already established pack. Similar to natal dispersal, we right-censored individuals that died, that had not yet dispersed at the end of data collection, that had gone missing from the pack with unknown fate, and that dispersed following pack breakup (Table S1). We applied a single FPPH model, which, due to the small sample size of known dispersers (i.e. 42 individuals), included both sexes, and used months since pack formation (for founders) or months since joining the pack (for immigrants) as time scale, and pack identity as a shared frailty component. We included number of "potential competitors" for the breeding position (i.e. number of non-dominant same-sex adults who are unrelated to the dominant individual of the opposite sex; McNutt & Silk, 2008), number of pups, dominance status of the individual, sex, population density, population sex ratio, rainfall, time since last reproduction, and biologically meaningful interactions in our full model (Appendix S5).

Pack breakup (model 3)

To examine the rate of pack breakup we right-censored packs that were either lost from the study or persisted at the end of data collection. We fitted a FPPH model with pack tenure length (months since pack formation) as time scale. We included number of pups, number of adults (i.e. pack size), whether or not all pack members were related, population density, rainfall, time since last reproduction, and biologically meaningful interactions in our full model (Appendix S6).

Dispersing coalition size (model 4)

We used individual, social, and environmental predictors to assess whether wild dogs would disperse alone or in coalitions of two or more same-sex individuals. To quantify correlates of dispersing coalition size, we performed separate analyses for natal dispersal and secondary dispersal. For natal dispersers, we applied a Poisson GLMM with predictors sex, number of pups, number of adults, number of same-sex siblings, mean age of same-sex siblings, population density, and meaningful interactions (Appendix S7) as well as the random term pack identity in our full model. For secondary dispersers, we estimated correlates of dispersing coalition size by running a Poisson GLMM with predictors sex, number of pups, number of same-sex adults, and two-way interactions (Appendix S7).

Predicting dispersal probability of missing individuals

We used knowledge of the factors (e.g. age, pack size, relatedness) influencing the decision to disperse, as inferred from confirmed dispersal events (models 1 and 2), to assign a dispersal probability to missing individuals. Specifically, we right-censored any missing individual on its second-last confirmed sighting and, given individual, social, and environmental factors associated with the last confirmed sighting within the pack, we estimated the probability that absence on the following sighting was due to dispersal. Our predictions thus returned the probability that a missing individual had dispersed from its pack, rather than having died. To predict this, we calculated dispersal probability as a function of the integrated dispersal rate over one time step, i.e. one month (Ergon, Borgan, Nater, & Vindenes, 2017) (Appendix S8). We assumed the probability of false absence (i.e. an individual was not seen, and so defined as missing, despite still with the pack) to be zero, for we confirmed absence during a minimum of three consecutive sightings to be defined as such.

RESULTS

Descriptors of dispersal and dispersing coalition size

African wild dogs started dispersing at 13 months of age with females and males showing the highest dispersal rate at 33 months and 37 months, respectively (when all other predictor variables were at mean values; Fig. 1A). For any given age, males were less likely to emigrate from the natal pack than females (estimated dispersal ratio = 0.7, Fig. 1A). The rate of secondary dispersal was an order of magnitude smaller than natal dispersal (Fig. 1C). Males were considerably less likely to exhibit secondary dispersal than females (estimated dispersal ratio = 0.6, Appendix S5).

Dispersing coalition size was larger for natal dispersers ($\bar{x}$ = 3.0, SE = 0.2) compared to secondary dispersers ($\bar{x}$ = 1.4, SE = 0.2; Appendix S7; Fig. S1). We did not observe significant differences in coalition size between the two sexes, either in natal or in secondary dispersing coalitions. Natal dispersing coalition size increased with number of same-sex candidate dispersers (β = 0.13, SE = 0.05) and decreased with increasing numbers of pups (β = -0.14, SE = 0.06). Of all natal dispersing coalitions, 49% of male and 35% of female coalitions included individuals born in multiple litters. Multi-litter dispersing coalitions were overall larger than single-litter coalitions (β = 0.24, SE = 0.06). Secondary dispersing coalition size increased with number of same-sex adults present in the pack (β = 0.37, SE = 0.15).

Natal dispersal

Individuals of both sexes were more likely to disperse when there were no unrelated individuals of the opposite sex in the pack (Fig. 1B, Appendix S4). Female dispersal rate decreased with increasing number of pups in larger packs, but increased with increasing number of pups in smaller packs (Figs 2A-B). Female dispersal rate showed a seasonal pattern with highest rates in March and lowest rates in September (Fig. 2D). Male dispersal

rate decreased with increasing number of pups in the pack and increased the larger the pack and the more same-sex siblings were present (Figs 2A-C). Male dispersal rate showed a seasonal pattern with highest rates in December and lowest in June (Fig. 2D). Dispersal rate of either sex were not affected by population density, population sex ratio, or rainfall. Furthermore, the effects of pack size and number of pups did not vary with season for either sex. Likewise, the interaction of number of same-sex siblings and whether or not all pack members of the opposite sex were related did not affect the dispersal decision. Tests of the PH assumption suggested that the effect of relatedness was not constant over time for either sex (i.e. their relative dispersal rate increased at older ages when they were related to all pack members of the opposite sex). We did not identify any other departures from the PH assumption in either sex. With an AUC males = 0.76 and an AUC females = 0.74, our final models can be regarded as good.

Secondary dispersal

Individuals were less likely to disperse a second time if they were dominant and if many pups were present in the pack. High numbers of potential competitors for the breeding position, resulting in lower probabilities of becoming dominant, were associated with a higher secondary dispersal rate (Fig. 2E). Secondary dispersal showed a seasonal pattern with highest rates in March and lowest rates in September (Fig. 2D). We found no sex difference in the effect of season. Population density, population sex ratio, and rainfall did not influence secondary dispersal. We did not find any violations of the PH assumption, and predictive performance of our final model was good (AUC = 0.77).

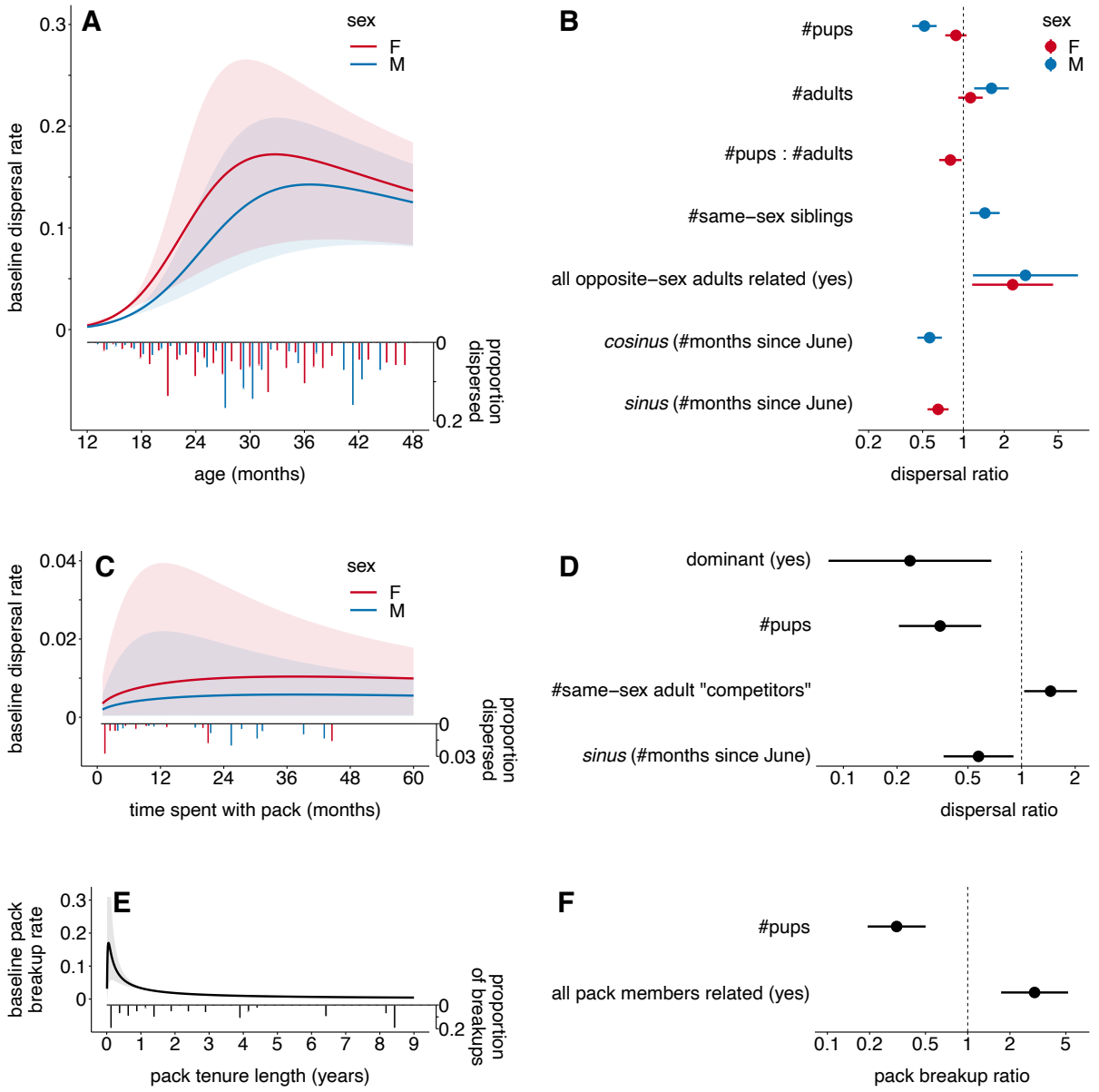

Figure 1: (A) Baseline dispersal function showing the rate of natal dispersal for male (blue) and female (red) African wild dogs as a function of age (when all other predictor variables were at mean values). (B) Dispersal ratios (DRs) showing effects of one-unit increases in standardised predictors and interactions on the rate of natal dispersal. DRs have a multiplicative effect on the baseline dispersal rate: DR>1 shifts the baseline dispersal curve upwards, which results in a higher dispersal rate compared to the "baseline" (for a given age and by holding all other predictors equal). The opposite applies for DR<1. (C) Baseline dispersal function depicting the rate of secondary dispersal for female (red) and male (blue) individuals as a function of time spent with the pack. (D) Effects of predictors on the rate of secondary dispersal. (E) Baseline pack breakup function showing the rate of pack breakup as a function of pack tenure length. (F) Effects of predictors on the rate of pack

breakup. In plots A, C, and E, observed proportions of dispersed individuals and pack breakups, respectively, are shown on separate *y*-axes. In all plots, shaded areas and error bars depict 95% confidence intervals. Baseline functions were best fitted with a log-logistic (A, C) or inverse Weibull distribution (E). In plot E, the upper bound of the confidence interval was truncated for visualisation purposes.

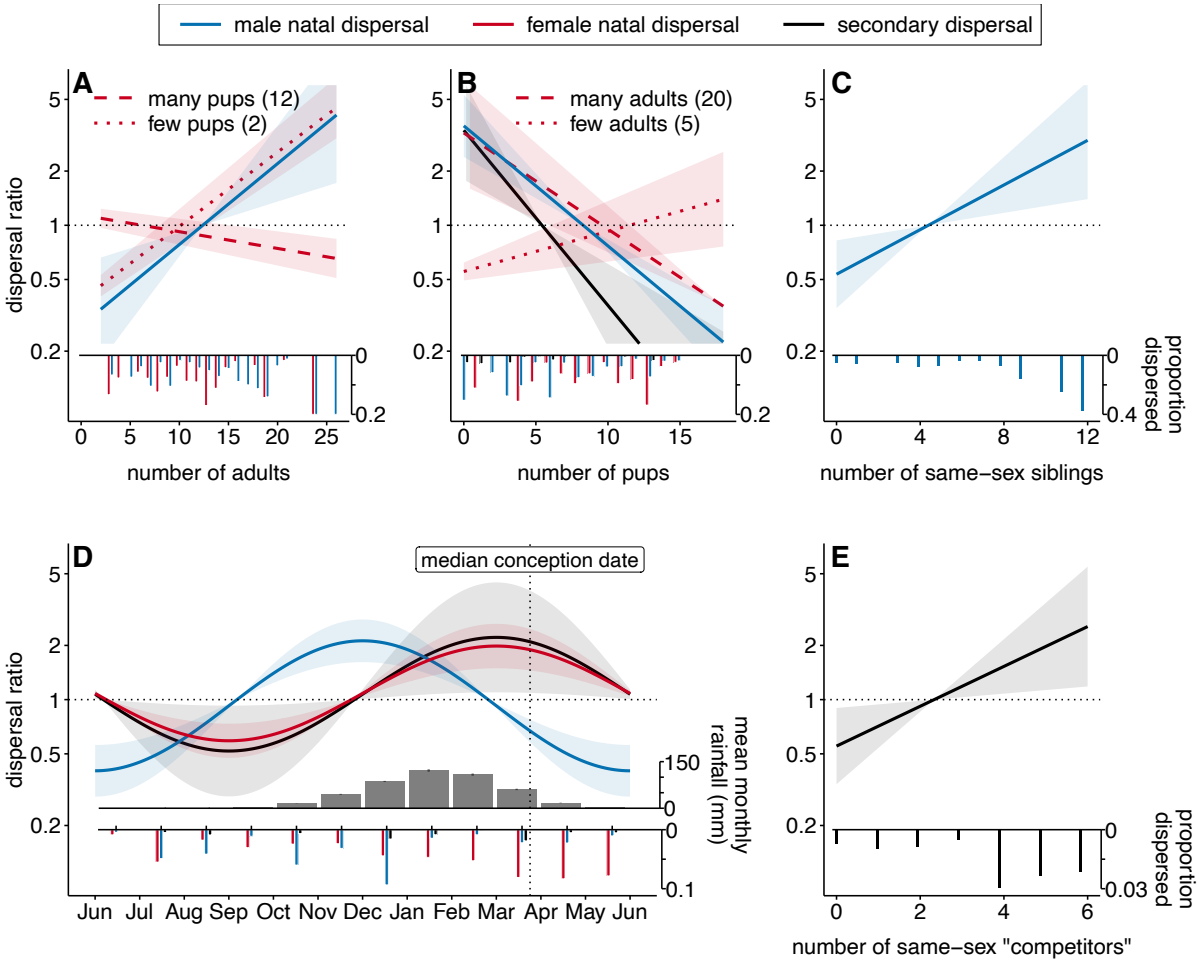

Figure 2: Effects of continuous predictors (A-E) on the rate of natal dispersal (blue for males, red for females) or secondary dispersal (black). Higher dispersal ratios result in a higher dispersal rate (see caption of Fig. 1). In (D), mean monthly rainfall from 1989 to 2019 and median conception date (McNutt et al., 2019) are shown for ease of interpretation. In all plots, observed proportions of dispersed individuals are depicted on separate *y*-axes.

Pack breakup

The rate of pack breakup was highest within the first year following pack formation (Fig. 1E) resulting in 60% of overall breakups occurring during this period (Fig. S2). After the first year (pack tenure > 1 year), pack breakup rate increased if all members (irrespective of sex) were related (Fig. 1F, Appendix S6). High numbers of pups present were associated with a lower pack breakup rate. Population density, rainfall, and season did not affect the rate of pack breakup. Predictive performance of our final model was good (AUC = 0.79), and we did not identify any violation of the PH assumptions.

Dispersal probability of missing individuals

A total of 96 females (31% of all known adult females born in the focal population) and 130 males (39%) disappeared from the study area after they had last been seen in their natal pack (Table S1). Predictions based on our model suggested that 18% of missing females (mean dispersal probability $\bar{x}$ = 0.18, SE = 0.01) and 25% of missing males ($\bar{x}$ = 0.25, SE = 0.02) likely dispersed from the natal pack. Individuals that went missing at two or three years of age were more likely to have dispersed than those that went missing at younger or older ages (Fig. 3A).

Predicted secondary dispersal probabilities for missing individuals (126 females, 138 males) suggested that 1% of females ($\bar{x}$ = 0.01, SE = 0.001) and 1% of males ($\bar{x}$ = 0.01, SE = 0.001) had dispersed. This indicates that the great majority of individuals that went missing from a pack other than their natal pack may have indeed died, rather than having dispersed a second time (Fig. 3B).

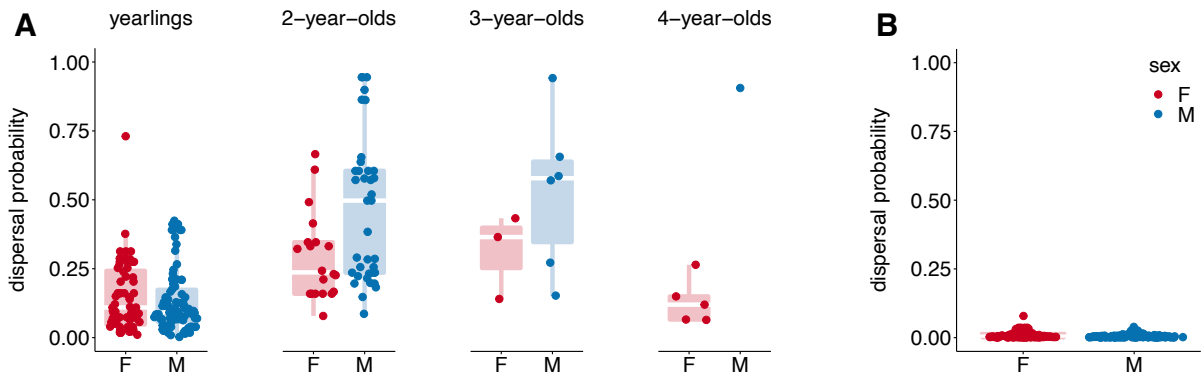

Figure 3: Predicted probabilities of natal dispersal (A) and secondary dispersal (B) for missing female (red) and male (blue) wild dogs. For natal dispersal (A), predictions are grouped by age of missing individuals. Boxplots show summaries of predictions with interquartile range. Dots represent predictions for each missing wild dog (226 individuals lost from natal packs, 264 individuals lost from packs other than natal pack).

DISCUSSION

We used individual, social, and environmental predictors associated with known dispersal events to assess and quantify the proximate causes of natal dispersal, secondary dispersal, and pack breakup in a free-ranging population of African wild dogs. We showed that interactions between these predictors affected each of the three dispersal types differently: Natal dispersal rate was highest in the absence of unrelated individuals of the opposite sex, secondary dispersal rate was mainly influenced by social status, and pack breakup rate was highest shortly after group formation and before first reproduction.

Our results, which showed that individuals of both sexes dispersed from their natal pack in the absence of unrelated individuals of the opposite sex, support the inbreeding avoidance hypothesis and the need of wild dogs to seek direct fitness outside the natal pack. While extra-pack paternity has been documented and males may thus obtain direct fitness benefits

without having to leave the natal pack (Girman et al., 1997; Spiering et al., 2010), subordinate females are rarely allowed to reproduce within their natal pack (Creel & Creel, 2002) and may only attain direct fitness through immigration in an unrelated existing pack or through the formation of a new pack. This may explain why males disperse at lower rates and at older ages than females. A similar dispersal pattern has been shown in meerkats (*Suricata suricatta*), a cooperative breeder with a social organisation similar to wild dogs, where males can attain extra-group paternity while temporarily roving outside the natal group (Young, Spong, & Clutton-Brock, 2007).

By delaying dispersal, (young) wild dogs of both sexes increase their indirect fitness by helping raising their younger siblings. Such fitness benefits appear to outweigh the costs associated with pup caring, such as food provisioning, for natal dispersal rate did not increase with increasing number of pups (except for females in small packs). These results are consistent with findings in the cooperatively breeding grey wolf (*Canis lupus*) (Gese & Mech, 1991) and red wolf (*Canis rufus*) (Sparkman, Adams, Steury, Waits, & Murray, 2011). However, as the per capita contribution towards pup provisioning decreases the larger a pack, (young) individuals may be more prone to disperse the larger a pack (this study). The observed increase in female natal dispersal rate with increasing numbers of pups in small packs may be explained by decreased benefits of cooperation (Clutton-Brock & Lukas, 2012). In such situations, females may disperse because a low helper-to-pup ratio can decrease inclusive fitness (Clutton-Brock et al., 2001; Cote, Clobert, & Fitze, 2007; Hamilton & May, 1977).

Contrary to our expectations but consistent with findings from northern Kenya (Woodroffe, O'Neill, et al., 2019), dispersal rate increased with natal group size (except for females in packs with few pups). As suggested by Woodroffe, O'Neill, et al. (2019), it thus appears that inbreeding avoidance and acquisition of direct fitness outside the natal pack outweigh potential feeding benefits associated with larger packs. However, it is not clear whether

474 larger packs have a greater per capita food intake (Creel & Creel, 2002), since McNutt
475 (1996b) suggested that competition for access to food increases with age and successive
476 litters. The observed positive relationship between natal dispersal and pack size may thus
477 potentially be attributed to resource competition arising from the social and age structure of
478 large packs. The effect of natal group size may further explain why male dispersal was more
479 pronounced at the beginning of the wet season when food availability is increased due to the
480 synchronised birth of impala calves (*Aepyceros melampus*) (Moe, Rutina, & Du Toit, 2007).
481 Males may thus compensate for diminished group hunting benefits (Creel & Creel, 1995;
482 Hubel et al., 2016) resulting from leaving their pack, by dispersing when prey that is
483 relatively easy for wild dogs to catch (Pole et al., 2004) is abundant. Females, on the other
484 hand, whose dispersal peaks in March, appear to delay dispersal from the natal pack to a
485 few months prior to the mating season (McNutt et al., 2019) to minimise costs of dispersal
486 (Bonte et al., 2012; Maag et al., 2019) and maximise mating opportunities.
487
488 Consistent with studies on other social carnivores (Fuller, 1989; Rood, 1987), rates of
489 secondary dispersal were lower compared to natal dispersal and were mainly influenced by
490 social status. If an individual (either a natal disperser or an immigrant) failed to acquire
491 breeding status in the new pack, its dispersal rate increased, underlying the ultimate
492 dispersal motivation of gaining direct fitness (Bowler & Benton, 2005) despite the costs
493 associated with dispersal (Bonte et al., 2012; Maag et al., 2019). Failure to attain dominance
494 in the new pack results in lower probabilities of breeding for females compared to males, for
495 in wild dogs, cases of shared paternity are more common than shared maternity (Creel et al.,
496 1997; Spiering et al., 2010) and may thus explain sex differences in the rate of secondary
497 dispersal reported here.
498
499 Packs with pups were unlikely to break up unless all remaining members were close
500 relatives, suggesting inbreeding avoidance and breeding failure as the main reasons for a
501 breakup (Girman et al., 1997; Rioux et al., 2011). Pack breakup rate was highest shortly

after group formation and before first reproduction, but our model failed to explain the underlying causes. Robbins & McCreery (2001) suggested that mate choice (i.e. group compatibility) can influence whether stable reproductive packs form. Hence, mechanisms governing mate choice of dispersing individuals and settlement success of newly formed packs represent an important focus for further studies.

We used information on the proximate causes of dispersal to assign a dispersal probability to individuals that were no longer sighted within their pack (missing individuals). We found that 18% of missing females and 25% of missing males had likely dispersed from the natal pack. In our sample of 226 missing adults (Table S1), these percentages correspond to 50 natal dispersers (17 females, 33 males). Based on the above reported average dispersing coalition size of 3 individuals, these figures translate to 17 dispersing coalitions and thus potentially up to 17 newly formed packs outside the study area. Given the order of magnitude of these numbers, failure to assign the correct fate to missing individuals would result in a misrepresentation of overall population dynamics, and consequently wrong management plans. Conversely, predicted secondary dispersal probabilities for missing individuals were overall low. These low predictions suggest that the fate of almost all secondary dispersers was known. In other words, mortality is the expected fate of missing individuals.

It is worth mentioning that some of our predictions may be biased low. On the one hand, our predictions treat a single missing dog equally to a dog that went missing with other same-sex dogs. Given that wild dogs usually disperse in coalitions rather than alone, a dog that goes missing with other individuals should be assigned a higher probability of having dispersed than a dog that goes missing “alone”. On the other hand, missing individuals may have either dispersed or died, and thus a more reliable prediction would involve estimating the joint likelihood of these mutually exclusive events. Therefore, using knowledge about the proximate causes of dispersal in an integrated framework that jointly estimates parameters

associated with mortality and dispersal (Barthold et al., 2016) will aid in predicting the fate of missing individuals more reliably and, finally, allow for a more accurate estimation of demographic rates.

In summary, our work, which aimed at quantifying individual, social, and environmental determinants of dispersal in African wild dogs, provides detailed information on the proximate causes of dispersal in a cooperative breeder. We showed marked differences in the effect of individual, social, and environmental predictors on the decision to disperse between males and females, as well as between natal dispersal, secondary dispersal, and pack breakup. These differences emphasise the importance to distinguish between different factors when assessing proximate causes of dispersal in a social species due to changing direct and indirect fitness consequences. Our work also provides a practical approach to the challenge of assigning a dispersal probability to missing individuals. This information can be used to distinguish between dispersal and death and, as such, constitutes a first step towards a reliable estimation of mortality rates. Accurate representation of key demographic rates is the foundation for reliable population models and appropriate management actions. Novel information on dispersal thus calls for the reassessment of population models that only marginally included this fundamental life-history process.

AUTHORS' CONTRIBUTIONS

G.C., D.M.B., and A.O. conceived the study; D.M.B. and G.C. designed the methodology; J.W.M., G.C., and D.M.B. collected the data; D.M.B. analysed the data and D.M.B., G.C., A.O., and J.W.M. interpreted the results; D.M.B. wrote the first version of the manuscript and all authors contributed substantially to the revisions.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xgxd254dd (Behr, McNutt, Ozgul, & Cozzi, 2020).

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